SEX RATIO AND WOMEN'S AGGRESSIVE COMPETITION

IN THE OUTER ISLANDS OF YAP

by

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ABSTRACT

Imbalances in the number of men and women—the adult sex ratio—are related to patterns of marriage and reproduction cross-culturally. Specifically, a shortage of men is associated with more divorce, more children out of wedlock, and more short-term, casual relationships. There are two competing hypotheses to explain this in the literature: one suggests this results from women's competition over scarce mates, and another suggests this results from men's increased mating effort when the returns to mating effort are the greatest. This dissertation tested whether women's mate competition drives this pattern. The research design was a natural experiment, comparing women's marital and reproductive histories, as well as self-reported aggressive competition, on two outer islands of Yap, which share a similar cultural history but differ in the sex ratio. The data show that women were not more aggressive when men were scarce, but sex ratio did appear to affect the consequences of aggressive competition. Sex ratio was also related to women's reproduction in ways that suggest that some men likely do exhibit more mating effort when there is a surplus of women. This dissertation adds to the growing literature on the adult sex ratio as a predictor of mate competition, highlighting that a scarcity of mates does not appear to predict women's aggression but suggests factors that might.

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CHAPTER I

INTRODUCTION

Guttentag and Secord's (1983) book *Too many women? The sex ratio question* popularized the important demographic and social consequences of imbalances in the adult sex ratio. Societies with too many women, where men are scarce, tend to have less stable marriages (e.g., Albrecht & Albrecht, 2001; Trent & South, 2003), a lower marriage rate (Angrist, 2002), more births out of wedlock (Barber, 2003), and perhaps also more violence (Barber, 2000; Barber, 2009).

There are two explanations for this in the literature. One suggests these patterns result from the interaction between men's mate preferences for low investing relationships with a variety of partners (e.g., Buss & Schmitt, 1993; Schmitt, 2003) and women's competition to offer traits men find attractive, because mates are few and far between (Pedersen, 1991; Schmitt, 2005). The expectation is that these patterns result from *women's competition* for mates, including aggressive competition (Campbell, 1995; Campbell, 2013), when mates are scarce.

The other hypothesis suggests these patterns result from feedbacks to the costs and benefits of mate competition when sex ratios are imbalanced. The logic follows the old adage that men are as faithful as their options—when mates are plentiful, men should pursue additional mating opportunities. Thus, these patterns of divorce, marriage rate,

and nonmarital births may be the result of increases in *men's mating competition* when there are too many women. This pattern has been confirmed in the anthropological literature for the stability of pair bonds (e.g., Blurton Jones, Marlowe, Hawkes, & O'Connell, 2000; Hurtado & Hill, 1992) and recently formally modeled (Kokko & Jennions, 2008). One corollary is that the returns to women's mating competition may be greatest when there are too many men.

This dissertation evaluates these two hypotheses in several ways. The second chapter examines the available evidence in the literature—whether women's mating effort and tactics of competition increase when mates are scarce, or whether they perhaps increase when the returns to mating effort are greatest—when there are too many men. To test whether a scarcity of men is associated with women's competition, I conducted field work in the outer islands of Yap using a natural experiment research design. Falalop, Ulithi and Falalop, Woleai share a similar culture, speak different dialects of the same language, but differ in the sex ratio—Ulithi has 'too many men' and Woleai 'too many women.'

The third chapter evaluates the results of this field work. It addresses whether women use aggression in mate competition by examining variables hypothesized to intensify it, including a scarcity of men. This chapter also evaluates the possible consequences of competition—whether aggression results in mating or offspring benefits, if perhaps it is associated with resource competition, rather than mate competition. The fourth chapter evaluates how imbalances in the sex ratio relate to Bateman's principles (Arnold, 1994), which indicate the fertility benefits to mating competition. Bateman's principles are considered to explain why sexual selection tends to be stronger on males

than females, and because imbalanced sex ratios are predicted to alter the costs and benefits of competition, this paper explores that relationship.

Women's mate competition is much less well understood than men's mate competition, and although the results of this dissertation suggest women's mating effort is complicated, this work illuminates the nature of women's aggression, marriage, and reproduction in the outer islands of Yap.

CHAPTER II

DO WOMEN COMPETE FOR MATES WHEN MEN ARE SCARCE? SEX RATIO IMBALANCES AND WOMEN'S MATE COMPETITION CROSS-CULTURALLY

Introduction

The goal of this chapter is to explore whether, and how, women compete over mates as a function of one variable hypothesized to intensify women's competition: the sex ratio. In the social sciences, the sex ratio has been measured as the number of reproductive aged men per 100 women (e.g., Guttentag & Secord, 1983), and researchers studying mating have used it as a window into men's and women's mate preferences and competition strategies (Pedersen, 1991; Schmitt, 2005). The reasoning has been—*sensu* supply and demand—a scarcity of mating opportunities should increase the intensity of competition among the surplus sex (Emlen & Oring, 1977). Also, it should reveal the preferences of the scarce sex, as they have more alternative potential mates available to them and may be in good position to exert their preferences (Guttentag & Secord, 1983; Pedersen, 1991). Newer theoretical models in biology predict the opposite relationship between a scarcity of mates and the intensity of competition; however, they predict increased competition when returns to mating effort are greatest—when there is a surplus of mates.

I review evidence from sociology, psychology, and anthropology to evaluate the support for two hypotheses about how sex ratio imbalances impact women's mate competition: a mate scarcity hypothesis and a frequency-dependent returns hypothesis. Throughout, I emphasize data from small-scale societies and cross-cultural samples, in an effort to provide as representative an account of women's behavior as possible (e.g., Henrich, Heine, & Norenzayan, 2010).

Sex Ratio in Sociology

The consequences of imbalances in the sex ratio were first popularized by Guttentag and Secord (1983) in their book *Too Many Women? The Sex Ratio Question*. They examine the demographic and social consequences of sex ratio imbalances in historical and contemporary datasets using a social exchange perspective, which emphasizes power and dependency as a result of market forces to understand romantic relationships (Cameron, Oskamp, & Sparks, 1977). This perspective proposes that the amount one person depends on his/her partner for satisfaction indicates the amount of power wielded by that partner, and this should be affected by the sex ratio. A member of the sex in short supply should be less dependent on his/her partner because they have more alternative potential mates available to them. Guttentag and Secord call this *dyadic power*, and propose that it allows the member of the sex in short supply to negotiate more favorable outcomes from their partner than they might otherwise be able to negotiate. However, Guttentag and Secord note a second concept also applies: most, if not all, societies are patriarchal, and thus women's ideal options—when potential husbands are plentiful and women have greater dyadic power—are yet constrained by men's greater *structural power*. Thus, they attempt to explain the effects of imbalanced sex ratios

across contemporary and historical societies as the result of an interaction between men's and women's dyadic and structural power.

Although pervasive in the sociology literature, this perspective makes many of the same predictions as the mate scarcity hypothesis, which I introduce next. The available data do not allow for distinguishing between them, but I reviewed it here due to its historical importance.

Sex Ratio in Evolutionary Psychology

Pedersen (1991) combined concepts from Guttentag and Secord's (1983) social exchange perspective with sexual selection theory; namely, he added the concept of mate choice and mate preferences to predict mating success in societies with an imbalanced sex ratio. He suggested, similar to previous researchers, that the sex in excess should compete intensely for members of the scarce sex, but added that this competition should take the form of the preferred marital traits of the scarce sex. For example, men tend to place greater emphasis on physical attractiveness in a long term mate than women do (e.g., Buss, 1989); thus, Pedersen hypothesized women compete to improve their physical appearance when men are scarce. This is similar to Guttentag and Secord's prediction regarding dyadic power, because it presumes the scarce sex has the power to drive mate competition toward their preferred domains (e.g., men's preference for attractiveness should increase women's competition to display it when men are scarce). It differs from the Guttentag and Secord perspective, however, by arguing that the resulting patterns reveal evolved sex differences in men's and women's mate preferences and corresponding competition tactics, rather than resulting from an interaction between dyadic and structural power. Thus, from this perspective, sex ratio imbalances are a

powerful tool to reveal underlying mate preferences and, to the extent a shortage of mates intensifies mating effort, reveal tactics in mate competition.

Explaining Variation in Sex Roles and Mating Effort

The term 'sex roles' is short-hand for the amount of reproductive effort allocated to mating versus parenting, which tends to vary between the sexes. Because this chapter reviews one variable hypothesized to affect the amount of effort women devote to mating competition—the sex ratio—it is important to note the other variable that has historically received the most attention to explain sex roles and mating effort: sex differences in parental investment. This argument begins by considering the consequences of sex differences in primary sexual traits. In humans, these sex differences include a difference in minimal obligatory parental investment required to reproduce (Trivers, 1972). For men, this is as brief as a few minutes, whereas for women, reproduction entails a minimum of months, and likely longer, for gestation and subsequent breastfeeding. These sex differences in the potential reproductive rates of males and females result in what are considered to be conventional sex roles (Clutton-Brock & Vincent, 1991)—namely, that males tend to be ardent in competing over choosy, discriminating females, who provide most of the parental care (Darwin, 1871).

Explaining sex roles as a consequence of sex differences in parental investment has been criticized in evolutionary biology as a logical fallacy, however, because 'sunk costs' in initial parental investment (e.g., expensive ovum) do not predict optimal allocation toward additional parental investment (e.g., gestation, lactation, and subsequent care, instead of competing for mating opportunities; Dawkins & Carlisle,

1976). Newer theoretical models have identified several variables that might instead explain the origin of sex roles—one of which is the sex ratio (Kokko & Jennions, 2008).

Sex Ratio and New Frequency Dependent Models

The sex ratio is hypothesized to have important consequences for mating and parenting effort because it creates frequency-dependent costs and benefits to competing and caring if there are different numbers of males and females in a population. That is, imbalances in the sex ratio should affect the costs and benefits of competition, such that if men are the scarce sex (a low sex ratio), the benefits of competition (additional mating opportunities among a surplus of women) increase faster than the costs (the risk of injury or death). These models remind us that every baby requires one mother and one father, and although men have a faster *potential* reproductive rate, their actual reproductive rate must, on average, be the same as women's—but only if the adult sex ratio is equal (Queller, 1997).

To illustrate—in a population where women are scarce (a high sex ratio), there are few benefits for a man leaving his mate to compete for new mating opportunities, if a new wife is hard to find. Contrary to older perspectives (e.g., Emlen & Oring, 1977; Pedersen, 1991), which argue that a scarcity of mates increases demand, these models indicate that if mates are scarce, competing is not necessarily the best option, especially if everyone else is competing, too. The abundant sex, rather than increasing the intensity of competition over the scarce sex, should *avoid* competition, since new mates are hard to find, and increase their parenting effort instead (Kokko & Jennions, 2008).

One caveat in applying this model to humans is that it was designed to explain the origin of sex roles, and may not apply to shorter timescales; feedback about frequency-

dependent costs and benefits may require longer periods, like generations, rather than the timescales under investigation by most social scientists. There is evidence, however, that human populations adjust to the frequency-dependent benefits of imbalanced sex ratios, in brief timescales, insofar as the sex of people's offspring (termed 'sex allocation') adjusts to the sex ratio of the population: in a preindustrial Finnish society, there were significantly more boys born in low sex ratio parishes, where the reproductive benefits of being among the rare baby boys are greater than being one of the relatively plentiful baby girls (Lummaa, Merilä, & Kause, 1998).

An additional qualification is that the sex ratio is not the only variable the models indicate should affect sex roles—variation in paternity certainty and sexual selection on males should, too (Kokko & Jennions, 2008). However, those literatures are beyond the scope of this review, and I will focus only on the sex ratio for the remainder of this chapter.

Whither Sex Ratio? A Note on Sex Ratio in Biology

Social scientists were not the first to predict that imbalances in the number of males and females in a population might affect mating dynamics. Emlen and Oring, in 1977, introduced the term *operational sex ratio* (OSR) as a measure of the intensity of competition over mates. The OSR consists of two components: the ratio of reproductive aged men to women that we have been discussing here—termed the adult sex ratio in biology—and an additional term for receptivity, which is the availability to mate and reproduce (e.g., Kvarnemo & Ahnesjö, 1996). That is, in humans, a woman is not 'available to mate' during her pregnancy—a new mating opportunity could not result in an additional pregnancy—but her husband's could. Including this term for 'availability

to mate' in the OSR captures additional information about parental investment and reproductive rates that vary between the sexes and between species, and may provide a more precise measure of the reproductive resources at stake.

The new models explaining the origins of sex roles, described previously, highlight important distinctions between the adult sex ratio and the OSR. First, the potential reproductive rate that is included in the calculation of the OSR—that second term—may not be as informative as the actual reproductive rate (Kokko & Jennions, 2008). In addition, biologists have until recently used the OSR and the adult sex ratio almost interchangeably in their experiments. Many studies manipulated the numbers of males and females in an effort to manipulate the OSR (e.g., Chipman & Morrison, 2013; Dreiss, Cote, Richard, Federici, & Clobert, 2010; Owens & Thompson, 1994). The discussion over the importance of the OSR relative to the adult sex ratio continues (e.g., Kokko, Klug, & Jennions, 2012). This chapter will focus on the adult sex ratio, so as to test predictions from the new frequency-dependent models, but also for pragmatic reasons. There are few studies examining the OSR in humans (e.g., Blurton Jones, et al., 2000; Hurtado & Hill, 1992; see also Marlowe & Berbesque, 2012), compared to a great many reporting relationships with the adult sex ratio.

Hypotheses

Mate scarcity hypothesis (Pedersen, 1991; Campbell, 2013). Following Emlen and Oring (1977), this hypothesis predicts a shortage of mates to increase the intensity of women's mate competition—in particular, competition to display traits attractive to men (Pedersen, 1991). Thus, given men's greater interest in short-term, casual relationships (e.g., Buss & Schmitt, 1993; Schmitt, 2003), this hypothesis predicts that women should

be more interested and willing to engage in these relationships when men are scarce (low sex ratio societies). Women should also increase their intensity of competition in additional domains preferred by men, including physical attractiveness (e.g., Buss, 1989) and perhaps resource competition (e.g., South, 1991). Additionally, women should compete using aggression when mates are scarce (Campbell, 2013).

Frequency-dependent returns hypothesis (Kokko & Jennions, 2008). New biological models predict the opposite relationship between a shortage of mates and competition: men and women each should compete most intensely when the returns to mating effort are greatest—when there is a surplus of mates. If everyone else is competing over scarce husbands in low sex ratio societies, it might pay women to devote more effort to parenting; if men are plentiful in high sex ratio societies, then the benefits that may accrue to women of mating effort (e.g., Brown, Laland, & Borgerhoff Mulder, 2009; Hrdy, 2000) should be relatively larger. According to this hypothesis, a shortage of mates should lead to *less* mate competition, whereas a shortage of mates should lead to *more* mate competition according to the mate scarcity hypothesis.

Ironically, although the two hypotheses predict opposite relationships between the sex ratio and the intensity of competition, they predict similar patterns for marriage rates and marital stability. The reason is they place different emphasis on evaluating mate competition as a function of mate preferences versus trade-offs. The mate scarcity hypothesis tests for the sex ratio to interact with marriage patterns, which should reveal sex differences in preferred amounts of parental investment (e.g., Buss & Schmitt, 1993) among the scarce sex. The frequency-dependent returns models are interested in these same patterns of parental investment because it should trade-off with levels of mating

effort, if human reproductive effort reflects either mating or parenting effort (e.g., Betzig, 1988). Thus, in high sex ratio societies where women are scarce, both perspectives expect men to devote more effort to caring (which might also be conceptualized as mate guarding), reflected by early and stable marriages. From an evolutionary psychological perspective, this occurs because women's scarcity allows them to exert their preferences for paternal investment (e.g., Buss & Schmitt, 1993); this also supports the frequency-dependent returns hypothesis, however, which predicts the same outcome as a consequence of the reduced payoff to mating effort, if new mating opportunities are rare in high sex ratio societies.

A Note on the Causes of Sex Ratio Imbalances

Population variation is ultimately due to three factors: births, deaths, and migration (Guttentag & Secord, 1983). The emphasis in this chapter is on the potential *consequences* of imbalances in the sex ratio, but across the world there appear to be different *causes* of imbalanced sex ratios. For example, the Amazonian region in Brazil contains large deposits of natural resources, drawing a fast growing number of men to work the mines to extract them (Roberts & Dodoo, 1995). In contrast, Chinese sex ratio imbalances are primarily due to sex-specific infanticide favoring boys, which is exacerbated by the country's one-child policy (Hudson & den Boer, 2004). In a cross-national sample, Schmitt and Rohde (2013) found sex ratio imbalances to be highly correlated with sex differences in mortality rates. This is likely the case in Colombia, where the very low sex ratios in some states are driven by excess male mortality due to violence rather than male migration (Jones & Ferguson, 2006).

Most of the research reviewed below is correlational, rather than experimental. As a result, we cannot conclusively determine if those findings are caused by sex ratio imbalances. Where available, I will highlight the results of experiments. For the remainder, there are two reasons we might suppose them to be linked. First, there are distinct causes of sex ratio imbalances across the world, and despite this, many variables show fairly consistent patterns. Second, all studies include a number of control variables, although these vary by study. Until we have a larger body of experimental work—and it is growing in psychology (e.g., Griskevicius, et al., 2012; Watkins, Jones, Little, DeBruine, & Feinberg, 2012)—this will remain a limitation of much sex ratio research.

Thus, I examine whether the available evidence supports the mate scarcity hypothesis or the frequency-dependent returns hypothesis, to understand how imbalances in the sex ratio relate to women's mate competition.

Analysis

There are several ways we might measure mating competition to test if it increases when mates are scarce (the mate scarcity hypothesis) or if it increases with a surplus of mates (the frequency-dependent returns hypothesis). First, I review measures which may indicate an overall intensity of mating effort, including the marital patterns, like marital stability, discussed previously, but also sociosexuality, mate poaching, and marriage systems. Then, I review specific tactics of mate competition, including aggression and mate choice competition, which should vary in frequency according to the intensity of women's mating competition, providing a test of our hypotheses.

The Sex Ratio and General Measures of Mating Effort

Marriage and Reproduction

A great deal of research in sociology examines the consequences of sex ratio imbalances for marriage and reproduction. They find a consistent general pattern, using a variety of measures: high sex ratio societies are associated with a greater proportion of the population marrying (Angrist, 2002; Albrecht, Fossett, Cready & Kiecolt, 1997; Cox, 1940; Lichter, McLaughlin, Kephard, & Landry, 1992; South & Trent, 1988); marriage at earlier ages (Kruger, Fitzgerald, & Peterson, 2010; South, 1988; Trent & South, 2011; Trovato, 1988); fewer divorces (Albrecht & Albrecht, 2001; Blurton Jones, et al., 2000; South & Trent, 1988; Trent & South, 1989; Trent & South, 2003); higher fertility rates (Fu, 1992; Schmitt & Rohde, 2013; South, 1988); and fewer births out of wedlock (Barber, 2001a; Barber, 2003; Fossett & Kiecolt, 1990; Fossett & Kiecolt, 1991). Thus, the general pattern is one of early, stable, and fertile marriages in high sex ratio societies, where men outnumber women, and unstable, lower-investing relationships in low sex ratio societies where there is a surplus of women.

As mentioned earlier, this is consistent with predictions from both perspectives. The mate scarcity hypothesis predicts that men can exert their preferences for short-term, low investing relationships in low sex ratio societies, because they have an excess of mating options—and women thus compete to display these traits to attract mates (Pedersen, 1991; Schmitt, 2005). The frequency-dependent returns hypothesis also predicts less paternal care and lower investing relationships in low sex ratio societies, because the returns to men's mating effort are higher, compared to when women are scarce (Kokko & Jennions, 2008). For these patterns, it is difficult to distinguish the role

of women's mating effort from men's, however, so perhaps additional measures provide a better test.

Sociosexuality and Mate 'Poaching'

Some studies have attempted to capture men's and women's mating effort more directly than marriage measures by using the Sociosexuality Orientation Inventory (SOI). Sociosexuality includes self-reported attitudes and behaviors that endorse casual sex (e.g., "Sex without love is OK;" "Number of sexual partners within the past year"), and sex differences in this measure are considered to represent men's greater exertion of mating effort compared to women (e.g., Schmitt, 2005). People who are interested in sex without commitment, thereby possessing an 'unrestricted SOI,' are more likely to have sex earlier in their relationships, maintain sexual relationships with multiple partners concurrently, and be in relationships that are less committed and investing (Simpson & Gangestad, 1991). They are also less attracted to people with good parenting qualities, preferring mates who are physically attractive, and are indeed more likely to be dating someone with those qualities (Simpson & Gangestad, 1992). Ethological and self-report investigations provide behavioral evidence that sociosexually unrestricted people engage in more mating effort, as measured by flirting behaviors (Bleske-Rechek & Buss, 2006; Simpson, Gangestad, & Biek, 1993) and by a greater number of lifetime sexual partners (Yost & Zurbriggen, 2006).

Thus, variation in sociosexuality is thought to reflect variation in mating effort (e.g., Schmitt, 2005), and likely captures some indication of the time and intensity a person expends attracting mates and mating opportunities. As such, women should report relatively unrestricted sociosexuality when men are scarce, according to the mate scarcity

hypothesis, whereas the frequency-dependent returns hypothesis predicts the opposite—that women should have an unrestricted sociosexuality when mates are abundant and the returns to mating effort are great.

An analysis of men's and women's combined average SOI scores across 48 countries found SOI was negatively related to a country's sex ratio, meaning men and women in low sex ratio countries reported they were comfortable with, and engaged in, more short-term relationships (Schmitt, 2005). Because men's and women's sociosexuality measures were combined, however, it is difficult to test predictions regarding women's mating effort. Additional evidence comes from an online survey replicating that study, which sampled over 200,000 people from 53 countries and analyzed men's and women's SOI scores separately (Lippa, 2007). There was a marginally significant trend for men's and women's SOI scores to negatively correlate with the national sex ratio, providing suggestive support for the evolutionary psychological hypothesis. A more recent study replicated these two, analyzing participants' SOI scores by U.S. state (Kandrik, Jones, & DeBruine, 2015). They found SOI scores were negatively related to the sex ratio for *both* men and women. This provides the first substantive evidence to distinguish between the hypotheses. However, to the extent sociosexuality captures general mating effort, it indicates conflicting support—variation in women's sociosexuality is consistent with the mate scarcity hypothesis; men's is consistent with the frequency-dependent returns hypothesis. Both men and women may compete more when there is a surplus of women.

Additional support for this pattern comes from a related measure analyzed by U.S. county. Among a representative sample of 12,571 people in 2002, both men and women

were more likely to report having concurrent, overlapping sexual partners if they lived in a low sex ratio county, relative to those living in a balanced sex ratio county (Adimora, et al., 2013). There is evidence, for men, that this pattern holds at the behavioral level: among the Hadza, when there were relatively more reproductive aged women in camp, compared to when there were fewer reproductive aged women in camp, men spent significantly less time with their kids (Marlowe, 1999). Notably, they did not appear to spend their time directly courting women; they were instead in discussion with other men, indicating perhaps that their competition took the form of negotiating alliances. Thus, although the data are weak but suggestive at the cross-national level, there is strong reason to believe that a surplus of women is associated with increased mating effort among men.

For women, the negative relationship between sociosexuality and the sex ratio may be limited to developed societies. Schacht and Borgerhoff Mulder (2015) tested this among the Makushi, who practice slash-and-burn horticulture in southwestern Guyana. They administered the SOI to 301 people across eight Makushi villages that varied in the sex ratio, and found men's responses to again be consistent with previous work, but not women's responses. As the sex ratio decreased—fewer men relative to women—men's SOI scores increased, while women's SOI scores remained stable across all eight villages. Thus, low sex ratios are consistently associated with mating effort among men, supporting the frequency-dependent returns hypothesis, but it is less clear how broadly sex ratio effects apply to women's mating effort.

Another window into mating effort is investigations of mate "poaching." These studies provide a more targeted measure of mating effort by examining the self-reported

frequency and circumstances of consciously attempting to attract someone else's mate (Schmitt & Buss, 2001). In his study of 53 nations, Schmitt (2004) asked nearly 17,000 participants about how frequently they had tried to attract someone already in a relationship. Analyzing men and women separately, he found support for the frequency-dependent returns hypothesis among women: women's mate poaching was more frequent when mates were scarce. Men's mate poaching was also more frequent in low sex ratio countries, providing additional evidence that men's mating effort increases with a surplus of mates. Thus, these data are consistent with the sociosexuality measures: women's mating effort appears to support the mate scarcity hypothesis, and men's appears to support the frequency-dependent returns. Again, however, these data derive from primarily developed nations, and it appears we need additional data from women in small-scale societies.

Marriage Systems as Indicators

Marriage systems are a cultural institution that can vary by society—e.g., whether polygyny is permitted or not—and may provide additional insight into mating effort from non-Western societies. Marriage systems can affect the variance in reproductive success, meaning variance in the number of offspring surviving to adulthood, which should indicate the intensity of competition over access to mates (Bateman, 1948; Brown, et al., 2009). The reason is that if a few men are able to monopolize a large number of women, leading other men to be shut out from reproduction entirely, the intensity of competition should be higher than if mating opportunities were more evenly distributed (Betzig, 1982).

Marriage systems do correspond to variance in reproductive success in humans: men have significantly higher variance in reproductive success than women in polygynous societies, relative to monogamous societies, where the variance in men's and women's reproductive success is similar (Brown, et al., 2009). Since the focus of this chapter is women's competition, polyandry might provide the converse for women—but because polyandry is rare, Brown, et al. (2009) were not able to report on whether women's reproductive success differs in polyandrous societies. However, this analysis will suppose that it may be associated with greater variance in women's reproductive success than other marriage systems, and is thus possibly linked to a greater intensity of mating competition among women.

Do imbalances in the sex ratio relate to marriage systems, which may serve as a society-level indicator of the intensity of competition? Consistent with the sociosexuality studies suggesting men exert more mating effort in low sex ratio societies, a random sample of cultures drawn from the Human Relations Area Files (HRAF) indicates polygynous societies are significantly more likely to have low sex ratios than non-polygynous societies (Ember, 1974). In contrast, using the Standard Cross-Cultural Sample—which consists of a representative sample of the world's cultures—Quinlan (2008) found no relationship. Additional evidence supports a relationship between polygyny and a low sex ratio, however. Pollet and Nettle (2009) investigated whether the proportion of the population polygynously married varied by the sex ratio in the 2002 Ugandan census. Using a representative sample, they found that low sex ratio districts had more polygynous marriages. Thus, if polygyny is associated with greater variance in reproductive success, men in low sex ratio districts are likely competing more intensely

than men in high sex ratio districts where women are scarce. This too suggests men's mating effort supports the frequency-dependent returns hypothesis.

Starkweather and Hames (2012) examined whether this pattern extended to women. Using the HRAF, they found polyandrous societies, which may be associated with higher variance in women's reproductive success and therefore more intense mate competition, were more likely to have a high sex ratio and an excess of men. In contradiction to the sociosexuality studies, this raises the possibility that some non-Western societies—those that practice polyandry—exhibit a positive relationship between the sex ratio and women's mating effort. This relationship is reinforced by one other study (Trent & South, 2011). Using a nationally representative sample in China, although on average infrequent, women in counties with relatively higher sex ratios reported being more likely to have had premarital sex and extramarital affairs (Trent & South, 2011; see also Trent & South, 2012). Thus, these two studies provide initial support for women's mating effort increasing with a surplus of mates in some non-Western societies.

An additional cultural practice related to female multiple mating is belief in partible paternity. Partible paternity is a cultural concept practiced by a number of lowland South Amerindian populations in which a baby is believed to be sired by multiple men, facilitating investment from the contributing fathers (Beckerman, et al., 1998). Two analyses suggest it is related to a low sex ratio: the first study modeled how this belief might have spread, and found it was likely to have caught on in communities with a relative surplus of women (Mesoudi & Laland, 2007); the second study found that, indeed, the presence of this belief is positively correlated with low sex ratio communities

(Ellsworth & Walker, 2015). These results also derive from non-Western, small-scale societies, but provide contrasting results to the polyandry and Chinese studies just discussed.

That polyandry and polygyny tend to be practiced in societies with an imbalanced sex ratio is perhaps unsurprising—it makes sense that excess men might be willing to accept a wife who is already married if they face the possibility of never reproducing otherwise, and vice versa for women. The conflicting results are between polyandry, associated with *high* sex ratios and that formally sanctions female multiple mating, and partible paternity, associated with *low* sex ratios and that likewise sanctions female multiple mating. It may be noteworthy that partible paternity, although involving investment on the part of multiple fathers (optimally two; Beckerman, et al., 1998), is not as great a commitment as marriage, as is the case in polyandry—echoing the pattern for marriage and reproduction that finds low investing relationships in low sex ratio societies. It is also possible that partible paternity functions to counteract this trend for low sex ratio societies to be associated with unstable and low investing relationships (e.g., Albrecht & Albrecht, 2001; Barber, 2003) by increasing investment (Beckerman, et al., 1998). Finally, although these data provide insight into how sex ratio imbalances relate to mating competition in non-Western societies, marriage systems are cultural ideals, not direct measures of behavior. This difference likely contributes to measurement error and conflicting patterns (Ellsworth & Walker, 2015).

In sum, across the various general measures of mating effort, there is a consistent pattern for men to engage in more short-term, casual relationships, to engage in more mate poaching, and to marry polygynously, in low sex ratio societies. This pattern is

consistent for cross-national, individual-level, and behavioral analyses—among developed and traditional societies alike. These measures provide strong support for men's mating effort conforming to predictions of the frequency-dependent returns hypothesis. The picture is more complicated for women. Studies of sociosexuality and mate poaching among developed populations suggest women increase their mating effort when men are scarce (e.g., Adimora, et al., 2013; Kandrik, et al., 2015; Schmitt, 2004; Schmitt, 2005), consistent with the mate scarcity hypothesis. In contrast, evidence from non-Western samples, including China (Trent & South, 2011) and polyandrous societies (Starkweather & Hames, 2012), suggests women may engage in more multiple mating, and thus likely more mating effort, in high sex ratio societies—although partible paternity societies indicate that this does relationship does not extend to all traditional societies (Ellsworth & Walker, 2015; Mesoudi & Laland, 2007). Indeed, sex ratio variation was unrelated to women's sociosexuality among the Makushi (Schacht & Borgerhoff Mulder, 2015).

These measures are approximations of mating effort, however. Perhaps a clear pattern for women will emerge by examining the frequency of specific mate competition tactics.

Sex Ratio and Women's Tactics of Mate Competition

Mating competition can take several forms. Darwin (1871) popularized two primary means of competition over mating opportunities: the tendency for males to compete with other males using physical aggression—what is often called male-male competition, or contest competition—as well as competition to display traits attractive to females, known as female choice, or mate choice (Cronin, 1991). In humans, both sexes

appear to compete both ways in some societies: qualitative evidence suggests women compete aggressively over men (Burbank, 1987; Campbell, 1986; Lepowsky, 1994; but see Ainsworth & Maner, 2012; Ainsworth & Maner, 2014) and vice versa (Benson & Archer, 2002; Chagnon, 1988; Wilson & Daly, 1985), but also that men and women compete to display traits attractive to the opposite sex (Buss & Dedden, 1990; Walters & Crawford, 1994), and that they both exhibit choosiness (Kenrick, Sadalla, Groth, & Trost, 1990; Stulp, Buunk, Kurzban, & Verhulst, 2013; Todd, Penke, Fasolo, & Lenton, 2007). Next, I review what we know about how imbalances in the sex ratio relate to the specific tactics women use in mate competition.

Physical Aggression

Most research on physical aggression has studied men, and for good reason—they are overwhelmingly more aggressive than women, at least as far as homicides go (see Daly & Wilson, 1990, for a comparison of same-sex homicides across a number of societies). Without a doubt, women can be aggressive, too, however. It is often directed toward men (Burbank, 1992; Hines & Fry, 1994; Pizarro, DeJong, & McGarrell, 2010), but when it is directed toward other women, the causes range from jealousy over a man (Lepowsky, 1994; Schuster, 1983), to defending her own or a friend's reputation (e.g., against accusations of promiscuity; Campbell, 1986), or protecting the honor of their neighborhood (Harris, 1994).

A number of studies have investigated whether sex ratio imbalances are associated with women's physical aggression, and none find a relationship. Campbell, Muncer, and Bibel (1998) examined women's same-sex assault rates across 34 criminal jurisdictions in Massachusetts, and found a small, but nonsignificant trend for there to be

more assaults in lower sex ratio districts. However, their measure of sex ratio incorporated the entire population, and including people of nonreproductive ages (i.e., children or postreproductive women) might explain this weak correlation. Thus, this was part of the motivation to conduct a carefully matched comparison of how sex ratio imbalances relate to aggression on two small island populations, as detailed in Chapter 3. To summarize—two outer islands of Yap, in the Federated States of Micronesia, had similar population sizes, spoke the same language, and shared the same general culture, but differed in the sex ratio—one had more men than women and the other had more women than men. Rates of women's reported physical aggression toward other women within the past year were nearly identical on the two islands, however, meaning that women's physical aggression was unrelated to the sex ratio. In addition, Schwartz (2006) examined 1,618 counties in the 2000 U.S. census, matched with FBI homicide data, and found no relationship between imbalances in the sex ratio and women's perpetration of homicide, which also suggests sex ratio imbalances are unrelated to women's aggressive competition. Note, however, that her dependent variable did not isolate women's same-sex homicide from aggression toward men.

The only studies that find any relationship between women's physical aggression and the sex ratio are two that have investigated women's involvement in crime, which includes assaults (Hitchell, 2004; South & Messner, 1987). They report a negative relationship between the sex ratio across nations and women-perpetrated crime rates, which would support the mate scarcity hypothesis. Crime measures include a number of extraneous variables, like property crimes, however, and thus are not a suitable test for this analysis.

Additional support for a null effect comes from an experiment examining men's and women's competitive responses to a hypothetical scenario wherein they witnessed an attractive rival flirt with their mate. Women who had been primed to believe that mates were scarce, relative to women who were primed to think that members of the opposite sex were abundant, were no more likely to say they would behave physically aggressively toward the rival (Arnocky, Ribout, Mirza, & Knack, 2014). Thus, there is as of yet no evidence to suggest that women become more physically aggressive when there is a scarcity *or* a surplus of men.

Indirect Aggression

Physical aggression is but one way to harm another person. Indirect aggression harms a competitor circuitously, potentially allowing for the aggressor to remain anonymous. Examples of indirect aggression include spreading vicious rumors about the other person, or making negative comments about their appearance to someone else (Green, Richardson, & Lago, 1996). Some researchers have found that women—in particular, adolescent girls—use indirect aggression more than boys (e.g., Lagerspetz, Björkqvist, & Peltonen, 1988), but a number of studies show that men and women report using a similar frequency of indirect aggression (e.g., Archer & Coyne, 2005; Hess, Helfrecht, Hagen, Sell, & Hewlett, 2010). Studies do find a sex difference in adults' *relative* frequency of use, however, indicating that a larger percentage of women's aggressive behavior is indirect (e.g., Österman, et al., 1998; Vaillancourt, 2013).

Does women's indirect aggression vary with the sex ratio? To my knowledge, only two studies have investigated this issue, and with mixed results. In Chapter 3, I analyzed self-reported indirect aggression, in addition to physical aggression, on the two

Micronesian islands that varied in the sex ratio, and found no difference between the islands. Single women did report a higher frequency of indirect aggression than married women—suggesting it is indeed likely related to competition for access to mates. The other study experimentally induced a perceived scarcity or surplus of mates by priming participants using fictitious magazine articles, and measured their response to a scenario in which they witnessed a highly attractive rival flirting with their partner (Arnocky, et al., 2014). In this case, women did report being significantly more likely to be indirectly aggressive toward the rival (e.g., make a joke about how ugly she was to her friends; tell her friends the rival was a jerk) when they believed mates were scarce relative to abundant. This finding provides experimental support for women increasing indirect aggression when mates are scarce. It may be that a shortage of men incites indirect aggression only in the case of mate-guarding or jealousy, explaining the contrasting results between the experiment and data from Micronesia. It may also be similar to the pattern for sociosexuality, which indicated a negative relationship with the sex ratio among samples from developed nations, but was unrelated to sex ratio among the Makushi. Clearly, we need additional research to understand if there is a pattern between women's indirect aggression and a shortage of mates.

Mate Choice Competition to Display Physical Attractiveness

Men find a number of traits attractive in a long-term mate, including mutual attraction/love, dependable character, and emotional stability (Buss, et al., 1990). Relative to women, men place greater importance on a partner's physical attractiveness (Buss, 1989). As a result, many studies have examined whether women use physical attractiveness to attract and retain mates. They do so by examining whether women find

a highly attractive peer threatening or intolerable (e.g., Buss & Dedden, 1990; Vaillancourt & Sharma, 2011) or by examining self- and peer-reports of the kinds of resources and traits over which women compete, wherein they identify trying to increase one's physical attractiveness (e.g., Buss, 1988; Cashdan, 1998). That this is a primary arena of women's competition makes sense, as good looks appear to be a salient feature for attracting men (e.g., Li, Bailey, Kenrick, & Linsenmeier, 2002; Marlowe, 2004).

Only a handful of studies have addressed whether women's competition to display attractiveness varies with the sex ratio (Barber, 1998a; Barber, 1998b; Pedersen, 1991), and these investigate societal trends as opposed to individual behavior. Pedersen (1991) presented a qualitative argument that the low sex ratios in the U.S. during the 1970s were associated with an increased emphasis on women's athletic fitness, as well as weight loss. He argued athletic fitness represents a more accurate indication of a woman's "reproductive efficacy" than a proxy like beauty, and argued that the proliferation of this fitness trend when men were scarce indicates support for increased competition in a low sex ratio society. Pedersen notes also that this 1970s trend was associated with feminist psychologies promoting women feeling in control of their bodies and less like they were catering to men's fashion whims; this logic is contradictory to an increase in the intensity of mate choice competition, however, because the nature of this competition is to increase attractiveness in the domains men find appealing.

Another analysis examined the waist-to-hip ratios of *Playboy* centerfolds from 1959-1978 and found quantitative support for Pedersen's (1991) assertion: models had fewer curves in years where men were scarce (Barber, 1998a). Similar data come from an analysis of the bust-to-waist ratio of *Vogue* models from 1949 to 1993: models were

curvier when there was a surplus of men (Barber, 1998b). Thus, there appears to be an historical pattern for low sex ratios to be associated with idealized figures that are less feminine. Again, although this is congruent with Pedersen's interpretation, it contradicts the mate scarcity hypothesis that women in low sex ratio societies are competing to display traits men find attractive (as men find feminine waist-to-hip ratios; Singh, Dixson, Jessop, Morgan, & Dixson, 2010). This pattern appears to be more consistent with the frequency-dependent returns hypothesis, given that women perceive high-quality feminine traits, like feminine faces, curvier busts, and lower waist-to-hip ratios, to be greater competitive threats than low-quality feminine traits (Fink, Klappauf, Brewer, & Shackelford, 2014).

This pattern for low sex ratios to be associated with ideal physiques that are less feminine might instead be consistent with increased competition by women over other things, like resources, given that variation in women's waist-to-hip ratios reflects a trade-off between estrogenic and androgenic hormones (Cashdan, 2008). This interpretation—that low sex ratios are related to increased competition by women over resources, not necessarily over physical attractiveness—is supported by an analysis of 117 countries which found low sex ratio societies were associated with a greater proportion of women participating in the labor force (South & Trent, 1988; see Durante, Griskevicius, Simpson, Cantú, & Tybur, 2012, for similar experimental results), and might also explain the negative correlation between the sex ratio and women's crime, which includes theft (Hitchell, 2004; South & Messner, 1987).

In sum, although not a direct test of individual behavior, these studies suggest that women might compete to display attractiveness in high sex ratio societies, when there is a

surplus of men, which is consistent with predictions from the frequency-dependent returns hypothesis. Given how salient competition to increase attractiveness is for women (e.g., Cashdan, 1998), future research should examine whether this positive correlation between the sex ratio and women's attractiveness competition exists at the individual level, as well as investigate how sex ratio imbalances relate to women's resource competition.

Mate Choice Competition to Display Resources

Although most mate selection research emphasizes women's greater interest in resources relative to men's, women's economic productivity is not irrelevant for men (e.g., South, 1991). For example, in response to the open ended question "If you were looking for a wife, what kind of woman would you want?" more Hadza men said they look for a hard working forager than all other traits mentioned, except for her character and her physical attractiveness (Marlowe, 2004). In addition, among the Shuar of Ecuador, men placed the same emphasis on a mate's resources as women did (Pillsworth, 2008). As such, perhaps women in some societies compete to attract high-quality mates using resources.

Dowry may represent one such cultural practice, in which a woman's family accumulates goods and resources to give to her and her husband on their marriage. Gaulin and Boster (1990) argue that in some societies—in particular, those with high social stratification and a prohibition on polygyny—dowry, represents female-female economic competition over well-resourced men. Without polygyny to dilute a husband's resources, women and their families may benefit reproductively by economically competing for men who control disproportionately large resources (Gaulin & Boster,

1997). If dowry represents female competition to attract high-quality husbands, perhaps dowry prices reflect the intensity of competition and provide a test of our hypotheses.

Two studies have investigated this question. In India, Rao (1993) sampled 141 households from 3 southern districts, and found that as the ratio of women to men who were of marriageable age increased, so did the average dowry payment. Thus, an increase in female competitors was associated with an increase in a woman's dowry, supporting the evolutionary psychological hypothesis. In Taiwan, Francis (2011) examined the consequences of the influx of mainlander Chinese to Taiwan after the government was overthrown by Mao Zedong in the Communist Revolution of 1949. Seventy-one percent of marriages in Taiwan involved payments on part of both the bride's family (dowry) and the groom's family (called bride-price). He found a similar relationship: as the number of men decreased, the ratio of bride-price to dowry payment decreased. Thus, there was a higher relative dowry payment by the bride's family when husbands were scarce. He found that this extended to highly educated men, arguably high-quality husbands, as predicted by the hypothesis: the more educated the husband, the lower the ratio of bride-price to dowry, indicating her family was willing to pay more relative to his family.

As Dickemann (1991) notes, payment on behalf of one's family is not identical to female-female competition engaged in by the woman herself. However, in societies where women have little autonomy, dowry may represent a plausible expression of the intensity of competition over husbands, especially considering that kin contribute to marriage contracts in many societies (Gaulin & Boster, 1997). One experiment aimed to test whether a perceived shortage of mates was associated with economic competition in

the West (Griskevicius, et al., 2012). In a college and community sample in the U.S., men, when primed to believe their campus and community had a high sex ratio, were more likely to report that they would take economic risks by saving less and incurring more debt, whereas women's spending was unrelated to a perceived scarcity or a surplus of mates (Griskevicius, et al., 2012). Risk may underlie the null effect for women's economic competition in this study, compared to the dowry analyses, which would be consistent with the null effects for another risky form of competition reviewed earlier—women's physical aggression (e.g., Arnocky, et al., 2014; Campbell, et al., 1998; see Chapter 3).

In conclusion, although qualitative evidence indicates women at times use physical aggression to compete for access to mates and in mate guarding, there is no evidence that a scarcity or a surplus of mates affects the frequency of this form of competition. Support for women's indirect aggression responding to sex ratio imbalances is mixed, with one experiment supporting the mate scarcity hypothesis (e.g., Arnocky, et al., 2014), and another study reporting no relationship (see Chapter 3). However, a surplus of men may be associated with an increase in competition to attract men via feminine physiques—at least, there is evidence that cultural ideals follow this pattern—providing suggestive support for the frequency-dependent hypothesis. Lastly, although it does not extend to American women's likelihood of engaging in risky spending, dowry prices do appear to reflect an increasing intensity of competition when husbands are scarce, supporting the mate scarcity hypothesis.

Conclusion

Both hypotheses to explain how sex ratio imbalances affect women's mating effort received some support, but neither was the clear winner. Corroborating the mate scarcity hypothesis, three measures indicated women's mating effort increases when mates are scarce: sociosexuality (Adimora, et al., 2013; Kandrik, et al., 2015)—albeit not among the Makushi (Schacht & Borgerhoff Mulder, 2015); mate poaching measures (Schmitt, 2004); and dowry payments (Francis, 2011; Rao, 1993). Attractiveness competition, as measured by figures in magazines, provided the only consistent support for the frequency-dependent returns hypothesis (Barber, 1998a; Barber, 1998b). The remaining measures indicated either mixed or no support. Both polyandry and partible paternity are practices presumably leading to women's multiple mating and thus greater mating effort, but one is associated with an excess of men (Starkweather & Hames, 2012), and the other with an excess of women (Ellsworth & Walker, 2015). Four studies (e.g., Campbell, et al., 1998; Schwartz, 2006), including one in a small-scale, traditional Micronesian society (see Chapter 3) and another an experiment (Arnocky, et al., 2014), suggest that imbalances in the sex ratio are unrelated to an increase in women's physical aggression. Only two studies investigated sex ratio imbalances and indirect aggression, and found mixed support for either the mate scarcity hypothesis (Arnocky, et al., 2014) or for no effect (see Chapter 3).

Two measures of women's mating effort were related with the sex ratio in developed nations, but unrelated when tested in small-scale, traditional societies. Neither Makushi women's SOI scores (Schacht & Borgerhoff Mulder, 2015) nor Micronesian women's indirect aggression (see Chapter 3) varied by the sex ratio, in contrast to support

for the mate scarcity hypothesis from developed nations (e.g., Arnocky, et al., 2014; Kandrik, et al., 2015). This may be consistent with other research, which indicates that sex ratio 'effects' are stronger in developed nations than in less developed nations (South & Trent, 1988). More specifically, Lippa (2007) found women's variability in sociosexuality decreased as gender egalitarianism decreased. Perhaps variation in women's mating effort is sensitive to men's ability to constrain women's behavior. It may be that developed societies provide an opportunity to witness women's mating effort with fewer constraints imposed by men; however, these societies are the least representative of human populations, including, most likely, ancestral human populations (Henrich, et al., 2010).

Indeed, women's behavior in small-scale societies may be comparatively constrained, but they do compete over men. Among the Tsimane, for example, conflicts over men (both adulterous husbands and single men) were named as the second-most frequent type of conflict women have with other women; the most frequent same-sex conflicts were social, involving conflicts over reciprocal contract defections and friendships, and the least frequent regarded food, including food theft and meat theft (Rucas, Gurven, Winking, & Kaplan, 2012). Future research should explore what *does* consistently predict variation in women's mating effort in traditional societies, if not the sex ratio, as well as how women's mating effort interacts with men's efforts to constrain it. Additionally, it may be that other predictors of women's mating competition apply consistently across developed and undeveloped societies alike (although Lippa's 2007 analysis suggests it may not). Whether this 'development effect' applies to women's mating effort more broadly than the sex ratio is another avenue for future research.

Only one pattern indicated unanimous support: men's mating effort—measured as unrestricted sociosexuality (e.g., Kandrik, 2015), concurrent sexual partners (e.g., Adimora, et al., 2013), mate poaching (Schmitt, 2004), and likelihood of marrying polygynously (e.g., Pollet & Nettle, 2009)—increased with a surplus of mates. Importantly, this pattern held for small-scale, non-Western societies (e.g., the Makushi; Schacht & Borgerhof Mulder, 2015), including a behavioral analysis among the Hadza that indicated men spent less time with their children when there were more women in camp (Marlowe, 1999). This increase in men's mating effort when there is a surplus of mates supports the frequency-dependent returns hypothesis.

However, as mentioned previously, this pattern has been interpreted as support for the mate scarcity hypothesis (e.g., Kandrik, et al., 2015; Schmitt, 2005), due to an emphasis on mate preferences and on competing for mates in ways the scarce sex finds attractive. Specifically, it supports the hypothesis that men prefer low investing relationships and women compete to offer these preferences when men are scarce and in demand. There are a number of reasons why this pattern is more consistent with an increase of mating effort by men, however.

First, as is evident in this review, we do not yet have a clear sense of how sex ratio imbalances impact women's competition. It remains a presumption that women's mate competition facilitates this pattern, especially if low sex ratio societies are associated with an increase in women's resource competition, rather than mating competition, as suggested earlier. Second, if sex differences in sociosexuality are interpreted to reflect sex differences in mating effort (e.g., Lippa, 2007; Schmitt, 2005), then variation in men's sociosexuality is an indicator of men's mating effort. Using that

logic, this review reinterpreted results that had previously been argued as supportive of the mate scarcity hypothesis, noting that men's data in those studies instead indicated support for the frequency-dependent hypothesis. This may be an incorrect interpretation of the sociosexuality measure, however, which is ultimately designed to measure willingness to have sex without commitment. Nevertheless, the remaining measures of men's mating effort (i.e., concurrent sexual partners, mate poaching, polygynous marriage, and behavioral trade-offs with direct paternal care) indicated consistent support at all levels of analysis for a negative relationship with the sex ratio. Third, Strategic Pluralism Theory, a primary hypothesis for explaining variation in men's and women's mating effort (Gangestad & Simpson, 2000), shares the same underlying logic as the biological models motivating the frequency-dependent returns hypothesis. Although Gangestad and Simpson emphasize the role of men's symmetry and its attractiveness to women, their argument is that symmetrical men, relative to less symmetrical men, should engage in more mating effort (and less symmetrical men in more parenting effort) because the returns to symmetrical men's mating effort are greater. The frequency-dependent returns hypothesis extends this argument to all men in low sex ratio societies, where the returns to mating effort are greater than in high sex ratio societies.

This review has raised several additional issues for future investigation. One outstanding issue remains conflicting measures of mate competition. Evolutionary psychologists place great emphasis on two factors in studies of mating: mate preferences, and understanding relationships on a temporal spectrum—i.e., explaining short-term, casual relationships versus long-term, committed relationships. Mate preferences are fundamental to understanding mate choice, but mate choice is only one way men and

women compete for mates (see, e.g., Andersson & Iwasa, 1996). In this case, measuring the intensity of competition as a function of preferences for temporal relationships (e.g., men's preferences for short-term relationships in low sex ratio societies versus women's preferences for long-term relationships in high sex ratio societies) - while informative, appears to have obscured the nature of the competition. One way forward is to unify the language of evolutionary psychology with that of evolutionary biology and anthropology. Presumably, the underlying variable of interest in studying relationships on a temporal spectrum is parental investment. Adopting this language, along with the concept of reproductive effort as a behavioral trade-off between mating effort and parenting effort (e.g., Betzig, 1988), might also bring clarity and consistency between the evolutionary disciplines. This is not a panacea, however—it remains difficult at times to distinguish whether a particular behavior represents mating effort or parenting effort (e.g., marriage and paternal care; Blurton Jones, et al., 2000; Marlowe, 1999; Winking, Gurven, Kaplan, & Stieglitz, 2009). Even so, the fact that the mate scarcity hypothesis and the frequency-dependent returns hypothesis predict the opposite relationship for the intensity of mating effort, but predict the same pattern for marriage, demands a reformulation.

Another issue raised by this review is the need for additional research on women's mating effort. It is obviously more complicated than men's mating effort. The only measure indicating a consistent pattern across developed and traditional societies alike was the null result for women's physical aggression. This suggests two avenues for future research: whether general measures of women's mating effort (like sociosexuality, mate poaching, and marriage systems) relate to specific tactics of women's mate competition (like aggression or mate choice competition to enhance attractiveness), as

they logically should, but did not, in this review; and whether variables other than the sex ratio are instead important in women's mate competition. Variation in male mate quality has received attention in the biology literature (e.g., Rosvall, 2011), and is predicted to affect the intensity of women's competition in evolutionary psychology, too (e.g., Campbell, 1995; Campbell, 2013).

In sum, this review found mixed results for how sex ratio imbalances affect women's mating competition. Some studies found it increased with a shortage of mates, as predicted by the mate scarcity hypothesis; some found it increased with a surplus of mates, as predicted by the frequency-dependent returns hypothesis; others found no relationship. This review raises important avenues for future research, including linking measures of women's general mating effort to the frequency of mate competition tactics, as well as whether sex ratio effects among women apply only to developed societies due to men's greater constraints on women's mating effort in traditional societies. Given the relevance of small-scale, traditional societies to understanding past human environments, understanding variables that *do* predict women's mating effort in these societies is of great interest. Also, given the conflicting pattern of results for women, we need additional research to clarify whether a shortage or a surplus of mates affects women's mating effort at all. It may be that other variables, like variation in male quality, are more important. Lastly, men's mating effort is consistently associated with a surplus of mates—indicating strong support for the relevance of frequency-dependent models to explain men's mating effort—and future research should clarify how men's and women's mating effort interacts to produce this pattern.

CHAPTER III

DO WOMEN USE AGGRESSION IN MATE COMPETITION? EVIDENCE FROM MICRONESIA

Introduction

Interest in sexual selection on females has increased in recent years (e.g., Clutton-Brock, 2007; Clutton-Brock, 2009; Fritzsche & Booksmythe, 2013; Stockley & Campbell, 2013). The question at the center of this discussion is not whether females compete (e.g., Cashdan, 1998; Pusey & Schroepfer-Walker, 2013; Richardson, 2005), but whether this competition is over mates (e.g., Amundsen, 2000; Hrdy, 2000; Rosvall, 2011). Humans may be a good species in which to examine sexual selection on females. Not only do women develop secondary sexual traits (e.g., Puts, 2010), but pair bonds suggest mates provide some benefit to women, although the nature of the benefit is debated (e.g., provisioning or protection; Hawkes, 2004; Smuts, 1992; Winking, et al. 2009). There is qualitative evidence that women compete over men—they compete to display traits men find attractive (Buss, 1988; Cashdan, 1998), and men are often the root cause of fights (Burbank, 1992; Campbell, 1985; Lepowsky, 1994)—but quantitative evidence linking women's aggression to competition over mates is harder to find (e.g., Campbell, Muncer, & Bibel, 1998; but see Arnocky, Ribout, Mirza, & Knack, 2014).

This study aims to quantitatively assess whether women's same-sex aggression is associated with mate competition in two ways. The first test examines whether several variables proposed to intensify women's competition over mates predict their self-reported aggressive behavior. One variable that should, *a priori*, reduce the intensity of mate competition is marriage. Unmarried women should experience more intense intrasexual competition over mates than women who are married, and indeed, single men commit more same-sex homicides than married men (Daly & Wilson, 1990). I also investigate age—in particular, youth—as a predictor of women's same-sex aggression. Adolescence signals entry into the mating arena, representing a woman's peak reproductive value and when she has the most to gain by mate competition (Campbell, 1995; Campbell, 2013). In addition, a scarcity of men, measured as a low adult sex ratio, is hypothesized to increase the intensity of women's mate competition (e.g., Cheney, Silk, & Seyfarth, 2012; Rosvall, 2011), although previous research has failed to find a relationship between adult sex ratio imbalances and physical aggression (e.g., Campbell, et al., 1998; Schwartz, 2006), finding women's physical aggression was instead associated with competition over scarce resources (Campbell, et al., 1998).

Hypothesis 1

If aggression is used in competition over mates, marital status, age (youth), and a scarcity of mates (low sex ratio) will be associated with an increased frequency of women's same-sex aggression.

Second, to explore whether aggression is associated with competition over mates, or whether it is instead associated with competition over resources, I examine its consequences. If aggression in women is sexually selected, it should have consequences

for mating opportunities (e.g., Vaillancourt, 2013), whereas if it is naturally selected, it should have consequences for offspring (e.g., Hrdy, 1979; Stockley & Bro-Jørgensen, 2011).

Hypothesis 2

If aggression is used in competition over mates, it will be associated with mating benefits, including the number of mates. If aggression is used in competition over nonmate resources, like food or status, it will be associated with increased resources for offspring.

I examine two measures of aggression: physical aggression, which involves attempting to directly physically harm another person (e.g., Archer, 2009) and indirect aggression, which involves attempting to harm someone circuitously (e.g., gossip damaging their reputation; Lagerspetz, Björkqvist, & Peltonen, 1988). I measure mating outcomes as the number of mates and benefits to offspring as fertility. I interviewed 60 women living on two small outer islands of Yap—Falalop, Ulithi and Falalop, Woleai—in the Federated States of Micronesia. The research design was a natural experiment examining the consequences of imbalances in the adult sex ratio; the two islands share a similar cultural history, people speak different dialects of the same outer island language, and both islands have similar population sizes, but they vary in the adult sex ratio.

Method

Participants

The outer islands of Yap are coral atolls, and consequently breadfruit, coconut, and taro are the subsistence staples, supplemented by reef and pelagic fish. Both Falaop,

Ulithi and Falalop, Woleai are home to the two high schools on the outer-islands, so there is a segment of the population who are wage earners, though most people continue to rely primarily on subsistence work. Political decisions remain regulated by traditional paramount, village, and lineage chiefs, although money is becoming increasingly important. Matrilineages and matriclans regulate marital behavior, as marriages should be clan exogamous, although people do marry within their clan, despite the stigma. Although most people practice Catholicism, premarital and extramarital relationships remain tolerated if discreet, and some people use contraceptives.

I conducted a census of the two islands to determine the adult sex ratio. Following Blurton Jones, Marlowe, Hawkes, and O'Connell, (2000), I calculated the adult sex ratio based on ages 15-45 for women, and modified the age range for men to include teenagers, including men ages 15-55, because teenage men father offspring in this society. The sex ratio in Ulithi was 118.9 men for every 100 women, and 86.2 men per 100 women in Woleai. Census records from 1987, 1994, 2000, and 2010 indicate that this imbalance has been stable, although it surely fluctuates, as people occasionally migrate among the islands and beyond.

I selected participants for interviews using a simple random sample, and all participants consented to participate. I provided either coffee or US $5, which approximates the cost of a bag of betel nut (a desirable stimulant), in appreciation for their participation. I interviewed 60 women, who ranged from 15 to 68 years old (M = 38.7 years; SD = 14.8). Of these, 2 women declined to answer the aggression questions (most likely due to loss of interest), and I am missing number of mates data for 1 woman,

and thus the total sample consists of 57 women for the mating benefits analyses and 58 women for the remainder. Thirty-six women (60%) were currently single.

Materials and Procedure

I measured aggression using the Richardson Conflict Response Questionnaire (Green, Richardson, & Lago, 1996), which asks about the frequency of 14 aggressive behaviors within the past year. I asked women to recall times when they had been angry at another women, to distinguish aggression from play fighting, and to think only of times when they had been angry at teenaged women or adult women, so as to exclude aggression directed toward men or children. Seven of the measures in the questionnaire constitute an indirect aggression subscale, inquiring about behaviors such as making up stories to get someone in trouble, or saying something negative about another person's appearance. Cronbach's alpha for this subscale was .76, which I summed to create an index of the frequency of indirect aggression within the past year. The remaining seven questions constitute a direct aggression scale. This measure included both physical aggression (e.g., attempting to hit someone with a hard object, like a stick or a rock) and direct verbal aggression (e.g., threatening someone). Although both forms of direct aggression were correlated ($r = .34$, $p < .01$), the variable of theoretical interest in this study is physical aggression. Thus, I created a physical aggression subscale consisting of the five direct physical aggression measures. Cronbach's alpha for this subscale was acceptable, $\alpha = .69$, which I summed for analysis. I asked about the number of live births to measure fertility. I measured the number of mates (e.g., Bateman, 1948), as other anthropologists have (e.g., Brown, Laland, & Borgerhoff Mulder, 2009; Smith, Bliege Bird, & Bird, 2003)—by summing the number of people with whom they reproduced.

Results

The frequency of total indirect aggression within the past year ranged from 0 to 23 (M = 7.6; SD = 5.7), and from 0 to 15 for the summed acts of physical aggression (M = 2.2; SD = 3.3). Mean fertility was 2.4 (SD = 2.2; range = 0-9) and mean number of mates was 1.1 (SD = 1.0; range = 0-5). Perhaps unsurprisingly, use of indirect aggression was moderately correlated with use of physical aggression (r = .29, p < .05). I coded both marital status and island sex ratio (low adult sex ratio versus high adult sex ratio) as dummy variables. Because the dependent variables for a number of hypotheses are frequency counts and the distribution thus non-Gaussian, I used negative binomial regressions (e.g., Hilbe, 2014).

Hypothesis 1 received mixed support: single women used more indirect aggression (M = 9.1; SD = 6.2; t(55.98) = 2.9; p < .05; see Figure 1) and marginally significantly more physical aggression (M = 2.75; SD = 3.9; t(51.58) = 1.97; p = .05) than married women ($M_{indirect}$ = 5.22; SD = 3.8; $M_{physical}$ = 1.27; SD = 1.7). As indicated in Table 1, however, when controlling for age and sex ratio, marital status alone predicted indirect aggression but not physical aggression. As you might expect if indirect aggression is associated with mate competition, it correlated with age (r = -.29; p < .05), but physical aggression did not (r = -.21; p > .05). Age was unrelated to aggression when controlling for marital status or sex ratio, however (Table 1). Counter to predictions, a scarcity of men was not associated with a higher mean aggression ($M_{indirect}$ = 7.3; SD = 5.3; $M_{physical}$ = 2.1; SD = 3.2), nor was a surplus of men ($M_{indirect}$ = 8.0; SD = 6.2; $M_{physical}$ = 2.3; SD = 3.56). Post-hoc, I also explored the possibility that if marital status is associated with the intensity of mate competition, perhaps only single women are

sensitive to imbalances in the sex ratio—but there was no interaction between sex ratio and marital status (see H1A in Table 1).

Because this was not a true experiment, it is difficult to determine the direction of causality for the primary marital status result. Are single women more indirectly aggressive because they are competing more intensely for mates than married women, or is it instead the case that women who use indirect aggression are more likely to be single? To explore this possible interpretation, I conducted additional post-hoc analyses.

First, if indirect aggression drives singlehood, you might expect highly aggressive women to be less likely to marry overall, if they are undesirable to men, but a binomial regression controlling for age (b = .11, se = .03, p < .001) indicates that indirect aggression is unrelated to a woman's likelihood of ever marrying (b = -.11, se = .07, p > .05). This means that indirect aggression neither worsened nor improved a woman's likelihood of marrying, casting doubt over the interpretation that male mate choice against indirectly aggressive women drives the marital status result. Next, since indirect aggression was unrelated to a woman's likelihood of marrying, I conducted post-hoc analyses to explore variables that *do* predict marrying in one's lifetime, and found an interaction between a woman's age and sex ratio. Figure 2 illustrates how sex ratio and age affected likelihood of marrying: on the high sex ratio island, where women were scarce, every woman in my sample married by a certain age (although she might have later divorced), in contrast to women on the low sex ratio island, where husbands were scarce. Lastly, I examine one final post-hoc test to evaluate the interpretation that aggression drives marital status by examining variation in indirect aggression on women's age at first marriage. This eliminates the confound of male mate choice, as each

of these women was selected as a marital partner. If aggression negatively predicts age at first marriage, it may indicate a mating benefit to women's use of indirect aggression, whereas a positive relationship between age at first marriage and aggression would be consistent with the interpretation that aggression drives marital status.

Women's mean age of first marriage was 24.94 (*SD* = 7.99, *n* = 32, range = 16-51 years old), although 1 woman appeared to be an outlier with an age of first marriage more than three standard deviations above the mean (51 years). Excluding this outlier, the oldest age of first marriage was 41 years. A negative binomial regression indicated that indirect aggression was unrelated to a woman's age of first marriage (b = -.06, se = .32, p > .05), again suggesting that it was not a general hindrance or help in marriage. However, when I explored the possibility of an interaction with sex ratio, several patterns emerged. Not only was the interaction between sex ratio and indirect aggression on age of first marriage significant (b = .07, se = .02, p < .001; see Figure 3), but there was a negative main effect of indirect aggression (b = -.10, se = .03, p < .01) and sex ratio (b = -.38, se = .15, p < .01) on age of first marriage. This pattern for high sex ratio to predict a younger age of first marriage is consistent with analyses of aggregate-level data (e.g., Kruger, Fitzgerald, & Peterson, 2010), but was not directly related to the sex ratio (b = .02, se = .09, p > .05). That is, neither indirect aggression nor sex ratio directly predicted the age of first marriage when entered as main effects in the model, but both predicted a younger age of first marriage after controlling for the interaction pictured in Figure 3.

To test Hypothesis 2, which aimed to understand the nature of the benefits to women's aggression, I examined whether women's aggression was associated with either higher number of mates or higher numbers of offspring. I included age as a control in

each of the models, because number of mates and fertility are both correlated with age (r_{MS} = .27; $p < .05$); $r_{Fertility}$ = .53; $p < .001$). As Table 2 indicates (models H2), only age predicted number of mates and fertility. Thus, similar to the previous analysis of indirect aggression on age of first marriage, there was no main effect of indirect aggression or physical aggression on number of mates or fertility. However, perhaps these measures, too, interact with sex ratio. I conducted post-hoc analyses to explore this, and the results are listed in Table 2 (models H2A). Neither indirect nor physical aggression interacted with sex ratio to result in higher number of mates, meaning neither form of aggression was associated with mating benefits when men were scarce. Physical aggression did result in differential fertility benefits, however (Table 2, H2A)—on the low sex ratio island, where men were scarce, women who were more aggressive had higher fertility than women who were less aggressive, and vice versa on the high sex ratio island (see Figure 4 for interaction plot, with aggression dummy coded for ease of presentation).

Discussion

Hypothesis 1 was supported—but only for marital status on indirect aggression. Single women were significantly more indirectly aggressive than married women, which suggests indirect aggression, but not physical aggression, is a form of mate competition in this society. Post-hoc analyses explored the possibility that the direction of causality for this result is reversed, but Figure 3 illustrates that if so, indirect aggression may only be a liability on the high sex ratio island—on the low sex ratio island, it was associated with a woman marrying earlier. In addition, indirect aggression did not reduce, or indeed enhance, a woman's likelihood of marrying, suggesting that the marital status result is not driven by male mate choice against indirect aggression.

If single women compete more intensely over mates using indirect aggression, but it does not increase their likelihood of marrying, what are the benefits to indirect aggression? Although other analyses indicate indirect aggression is effective—it decreases the attractiveness of a competitor, for example (Vaillancourt, 2013)—Hypothesis 2, which tested for mating benefits to aggression, was not supported. That is, if indirect aggression is used in mating competition, it did not result in an additional number of mates in this study. Although this raises the possibility that indirect aggression is unrelated to mating competition, it more likely indicates that number of mates is a poor currency for measuring mating benefits to women, for several reasons. First, other measures, including mate quality, are hypothesized to be more important than the number of mates for sexual selection on females (e.g., Forsgren, 2011; Rosvall, 2011; but see Cain, 2014). Second, indirect aggression does result in proximate competitive benefits (Vaillancourt, 2013), and these may translate into a higher quality mate, if not additional mates. Also, after controlling for the interaction with sex ratio in Figure 3, this study found that indirect aggression predicted a younger age at first marriage, which presumably reflects successful mate competition. Together, these suggest that indirect aggression results in mating benefits to women, but that mating benefits to women may be best measured in ways other than number of mates.

Hypothesis 1 was only partially supported, however. Although indirect aggression correlated negatively with age, as predicted if it is associated with mate competition, only marital status remained significant when age and sex ratio were included in the model. Also, none of the three variables predicted women's physical aggression, which suggests that if physical aggression is used in women's mate competition (as qualitative evidence

suggests; Burbank, 1992; Campbell, 1986), it is facultative (e.g., Campbell, et al., 1998), rather than predictable. The null result for sex ratio on women's physical aggression is consistent with two other cross-sectional studies (Campbell, et al., 1998; Schwartz, 2006) and one experiment (Arnocky, et al., 2014). The null result for sex ratio on women's indirect aggression, however, contrasts with one experimental finding in a Western population (Arnocky, et al., 2014). Nevertheless, this finding is consistent with another analysis of women's mating effort in a non-Western, traditional society, which found null effects of sex ratio on women's sociosexuality—her tendency to engage in casual, rather than committed, relationships—and which presumably reflects some amount of mating effort (Schacht & Borgerhoff Mulder, 2015). Thus, it may be that sex ratio effects on women's competition are stronger in developed nations (e.g., Lippa, 2007; Schmitt, 2004; see Chapter 2). It may also be that mate quality, again, is more important for women's competition than the number of mates.

Although a shortage of mates did not predict an increase in either type of women's same-sex aggression, it did affect women's mating in other ways. Sex ratio and age interacted to affect her likelihood of marrying, as illustrated in Figure 2. All of the women in my sample married by a certain age on the high sex ratio island, which is consistent with two interpretations currently in the literature (e.g., see Chapter 2): women in high sex ratio societies, because they are scarce, can better achieve their mate preferences for committed relationships (e.g., Buss & Schmitt, 1993; Pedersen, 1991; Schmitt, 2003; Schmitt, 2005) compared to low sex ratio societies; or, men engage in more mate guarding in high sex ratio societies, because women are scarce (e.g., Blurton Jones, et al., 2000; Hurtado & Hill, 1992).

Three expected relationships were only present once interactions with the sex ratio were controlled—a younger age of first marriage in the high sex ratio community (expected given previous research; e.g., Kruger, et al., 2010); for indirect aggression to be associated with a younger age of first marriage, if it represents mate competition; and the positive relationship between physical aggression and fertility. Each of these main effects emerged only after controlling for interactions with the sex ratio. On the surface, these results failed to replicate the main effects predicted by aggregate-level data. What this patterning reveals, however, is that the sex ratio affected the costs and benefits of aggressive competition. The value of indirect aggression for age of first marriage, and physical aggression for fertility, depended on the sex ratio—both types of aggression appeared to benefit women on the low sex ratio island but cost women on the high sex ratio island. The predicted relationships only emerged once the different payoffs to these behaviors were controlled. Far from a failure to replicate, these data reinforce the role of imbalances in the adult sex ratio to affect the returns to competition (e.g., Kokko & Jennions, 2008). As they resulted from post-hoc analyses, however, future research should validate them in other populations.

Contrary to Hypothesis 2, physical aggression did not benefit a woman by increasing her number of mates or her fertility—but physical aggression did predict fertility on the island were men were scarce, and it did predict fertility once this sex ratio interaction was statistically controlled. Fertility results from many factors, and although it only arguably reflects greater access to resources in a subsistence society, Figure 4 indicates a clear interaction effect. Although by no means established, it is plausible this interaction is a function of paternal investment, which may affect the intensity of

women's resource competition. That is, where women's expectation of paternal investment is low—as it appears to be in low sex ratio societies (Albrecht & Albrecht, 2001; Barber, 2003; Marlowe, 1999; Trent & South, 1989), including this one (see Chapter 4)—women may compete directly over resources for offspring, compared to contexts where paternal investment is expected to be higher. This interpretation, that women's physical aggression appears to be naturally rather than sexually selected, echoes the conclusions of another study which found that the percentage of unemployed women and women on welfare were better predictors of women's same-sex assault than a scarcity of men (Campbell, et al., 1998).

In sum, this research provided quantitative support that women's indirect aggression is used in mate competition, and although it may not improve the likelihood that she marries, or her number of mates, women who are indirectly aggressive marry at a younger age once sex ratio interaction effects are controlled—because indirect aggression appears to be especially effective if men are scarce. Age also correlated with indirect aggression, as predicted by previous research, but it appears this was driven primarily by marital status. A shortage of men was unrelated to women's indirect and physical aggression—consistent with previous research, but contrary to expectations in the literature—suggesting that the quality of mates may be more important for women than the number of mates. Thus, imbalances in the sex ratio did not predict the frequency of women's competition, but it did affect the costs and benefits of aggression. Finally, although physical aggression did not result in higher fertility overall, it did on the low sex ratio island, where resources for offspring may be particularly scarce, relative to the high sex ratio island.

Table 1

Hypothesis 1: Predictors of the Intensity of Women's Mate Competition

	Indirect Aggression			Physical Aggression		
Predictor	*b*	*se*	CI	*b*	*se*	CI
H1:						
Intercept	2.46*	.46	[2.56, 3.38]	1.92	1.08	[-.26, 4.28]
Marital status	-.44*	.21	[-.88, -.01]	-.62	.50	[-1.56, .36]
Age	-.01	.01	[-.02, .01]	-.02	.02	[-.05, .02]
Sex ratio	.03	.20	[-.37, .43]	-.19	.48	[-1.16, .76]
H1A:						
Intercept	2.38*	.59	[1.23, 3.56]	1.05	1.36	[-1.68, 4.12]
Age	-.01	.01	[-.02, .01]	-.01	.02	[-.05, .03]
Sex ratio (SR)	.07	.27	[-.47, .60]	.21	.63	[-1.12, 1.49]
Marital status	-.32	.66	[-1.60, .98]	.66	1.51	[-2.38, 3.81]
Marital status * SR	-.09	.43	[-.95, .76]	-.91	1.00	[-3.00, 1.16]

Note. * $p < .05$, two-tailed. See text for details about the hypotheses.

Table 2

Hypothesis 2: The Consequences of Aggression for Benefits to Mating versus Offspring

	Number of Mates			Fertility		
Predictor	*b*	*se*	CI	*b*	*se*	CI
H2: Main effect Indirect						
Intercept	-.91	.49	[-1.91, .01]	-.72	.43	[-1.61, .13]
Age	.02*	.01	[.003, .03]	.04***	.01	[.02, .06]
Indirect Aggression	.02	.02	[-.02, .07]	-.08	.02	[-.05, 03]
H2: Main effect Physical						
Intercept	-.57	.41	[-1.42, .22]	-.77	.38	[-1.58, -.01]
Age	.02	.01	[.000, .03]	.04***	.01	[.02, .06]
Physical Aggression	-.02	.04	[-.11, .06]	-.01	.04	[-.08, .07]
H2A: Indirect * Sex ratio						
Intercept	.44	.66	[-.88, 1.71]	-1.34	.74	[-2.82, .07]
Age	.01	.01	[-.003, .03]	.04***	.01	[.02, .06]
Indirect Aggression	.06	.07	[-.07, .20]	.07	.07	[-.06, .21]
Sex Ratio	-.22	.46	[-1.14, .68]	.44	.37	[-.29, 1.18]
Indirect * Sex Ratio	-.03	.05	[-.12, .06]	-.05	.04	[-.14, .03]
H2A: Physical * Sex ratio						
Intercept	.02	.66	[-1.30, 1.28]	-1.23*	.56	[-2.35, -.16]
Age	.01	.01	[-.01, .03]	.03***	.01	[.02, .05]
Physical Aggression	.15	.14	[-.12, .38]	.32**	12	[.09, .57]
Sex Ratio	-.24	.32	[-.89, .39]	.47	.25	[-.02, .95]
Physical * Sex Ratio	-.13	.11	[-.39, .06]	-.25*	.10	[-.46, -.07]

Note. * $p < .05$, ** $p < .01$, *** $p < .001$, two-tailed.

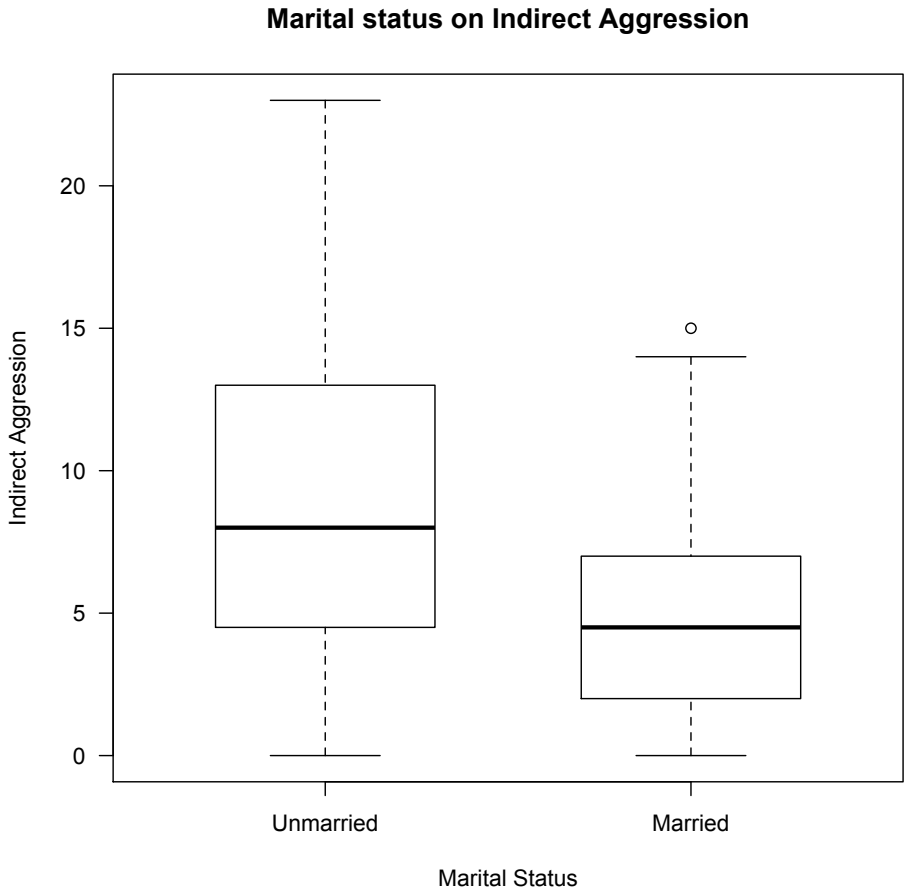

Figure 1. Marital status on indirect aggression.

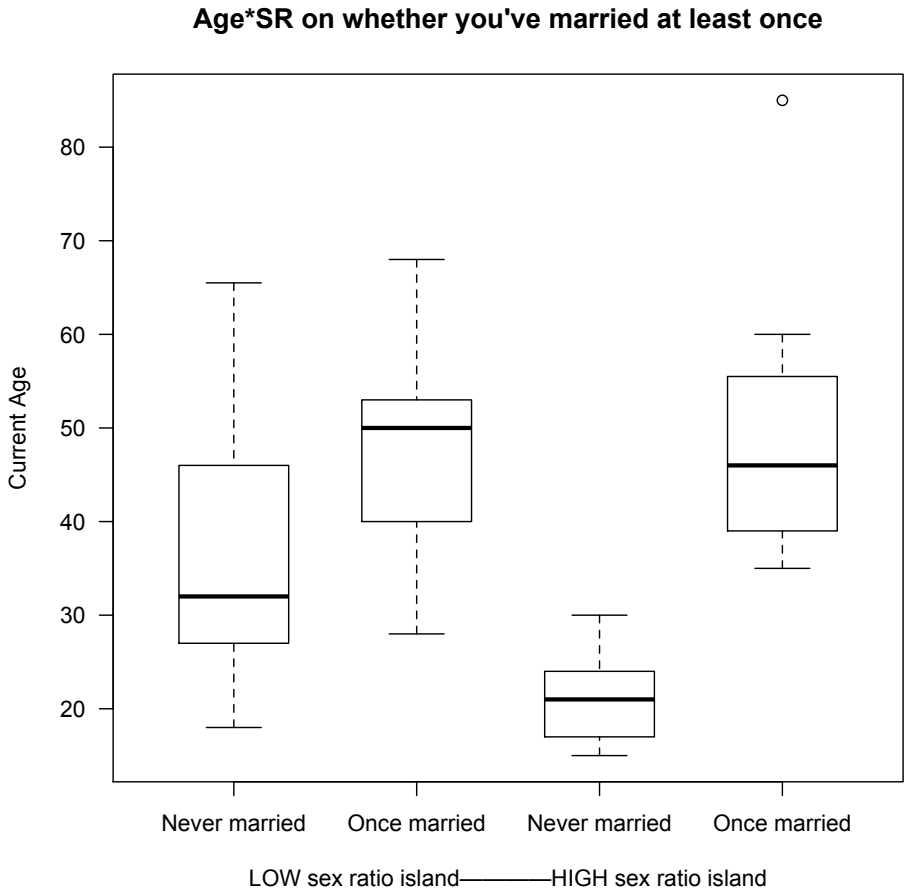

Figure 2. Interaction between age and sex ratio on whether you marry.

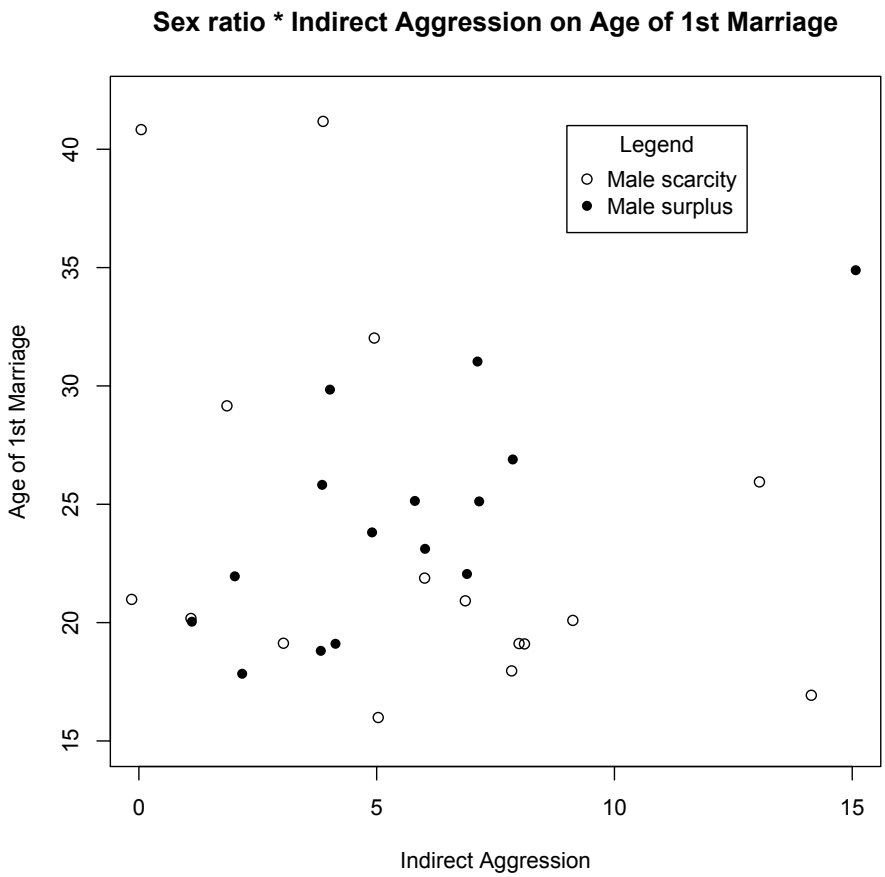

Figure 3. Interaction between sex ratio and indirect aggression on age of first marriage.

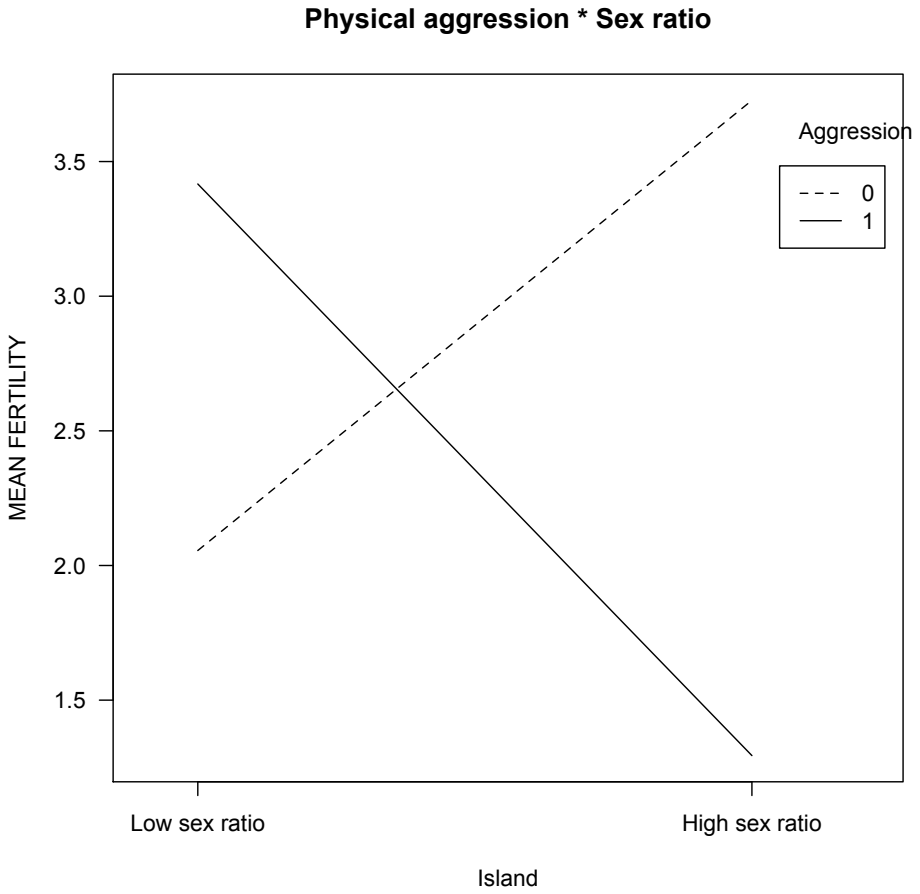

Figure 4. Interaction between physical aggression and sex ratio on mean fertility. For presentation, physical aggression was dummy coded, such that women who were not aggressive within the past year were coded as 0, and women who reported 1 or more instances of same-sex physical aggression were coded as 1

CHAPTER IV

ADULT SEX RATIO AND BATEMAN'S PRINCIPLES IN MICRONESIA

Introduction

Bateman (1948) is often credited with explaining why sexual selection tends to be stronger on males than females (e.g., Arnold & Duvall, 1994; Jones, 2009; Wade, 1979; though see Snyder & Gowaty, 2007). In doing so, he derived three principles (Arnold, 1994): first, that variance in male fertility (and likely reproductive success) tends be larger in males than females; second, that variance in male mating success (the number of partners with which an individual reproduces) tends to be larger than female variance in mating success; and third, the correlation between fertility and mating success is stronger in males than females. This third principle, known as the Bateman gradient, explains the conventional sex difference in sexual selection, because a steep Bateman gradient indicates a direct fitness benefit to acquiring additional mates (e.g., Kokko, Klug, Jennions, & Gaillard, 2012).

Variation in the adult sex ratio may have important consequences for sex roles, including altering the payoffs to competing for additional mates rather than providing parental care (Kokko & Jennions, 2008). In addition, a review of Bateman's principles in humans suggests that they vary between societies as well as between the sexes (Brown,

Laland, & Borgerhoff Mulder, 2009). The goal of this study is to examine how Bateman's three principles vary in one society as a function of the adult sex ratio.

Method

Study Population

The research design was a natural experiment. Two outer islands of Yap (Falalop, Ulithi and Falalop, Woleai), located in the Federated States of Micronesia, had similar population sizes, a shared cultural history, and spoke different dialects of the same outer island language, but differed in the adult sex ratio. Government census data from decades past indicate that, although the islands are not closed populations—it fluctuates whenever the irregular government field trip ship passes through—this sex ratio imbalance has remained consistent over the decades, although the cause remains unclear. My census during a 2012 field session indicated there were 118.9 men for every 100 women on Ulithi and 86.2 men per 100 women on Woleai. I have included men ages 15-55 and women ages 15-45 in calculating the adult sex ratio, following Blurton Jones, Marlowe, Hawkes, and O'Connell (2000), except I additionally include teenaged men ages 15-19, because they father children in this society. Due to their remoteness, the coral atolls outside Yap remain primarily horticultural subsistence societies, although most people supplement gardened food with canned meat and rice purchased with remittances or from the handful of government jobs on each island.

Catholicism is the dominant religion on the islands, and although the church has sanctions against contraception, some women use birth control pills provided by the dispensaries. Thus, some of these data reflect the results of reproductive decisions. Monogamous marriage is the ideal, but affairs are not uncommon.

Participants and Procedure

I randomly sampled 30 men and 30 women from each island for interviews, although for this analysis, I only have data for 58 men and 59 women. Men ranged in age from 17 to 76 (M = 37.9; SD = 15.1) and women ranged from 15 to 85 years old (M = 39.0; SD = 16.1). Note that the data are not completed reproductive histories, and people's ultimate reproductive trajectories may be different.

Following the Brown, et al. (2009) analysis of human populations, I measure number of mates as the number of individuals with whom someone reproduced. I measured fertility by asking about the total number of live births.

Results

Mean fertility was 2.5 (ranging from 0 to 15; SD = 2.74), and sex differences in the variance in fertility—Bateman's first principle—were marginally significant (var_M = 9.24; var_F = 5.94 for women; F = 1.55, p = .10). As is evident from Table 3, this was driven by the low sex ratio island, and indeed one man's fertility was more than 3 standard deviations above the mean. Removing this outlier removed any general sex difference in variance in fertility (F = 1.1; $p > .05$) as well as a sex difference on the low sex ratio island (F = 1.47; $p > .05$). However, because imbalances in the adult sex ratio—in particular, low sex ratios where women outnumber men—are predicted to create frequency-dependent benefits for males to counter-intuitively increase competition with an excess of mating options (Kokko & Jennions, 2008), this data point is relevant. I will note its effects on the results, however.

Contrary to Bateman's second principle, which predicts sex differences in the variance of mating success, the variance in men's (1.05) and women's (1.03; F = 1.02; p

> .05) number of mates was similar—although again, adult sex ratio appears to affect this (see Table 1). Men on the high sex ratio island were marginally significantly more likely to vary in mate number, whereas women and men on the low sex ratio island varied in their number of mates similarly. Without the male outlier on the low sex ratio island, however, women have significantly higher variance in number of mates ($var_F = 1.55$) than men ($var_M = 0.6$; $F = 0.38$; $p < .05$).

Figure 5 illustrates the relationship between fertility and number of mates—Bateman's third principle—for men as a function of the adult sex ratio; Figure 6 illustrates this relationship for women. The plots are best characterized by an interaction effect between sex and the adult sex ratio—sex ratio imbalances affect men and women differently. For men, the effect of number of mates on fertility (save the one outlier) is nearly identical between the two islands. For women, there are two clear patterns. On the low sex ratio island, where men are scarce, some women (all unmarried at the time of those births) have children by different men, whereas the remaining women on the low sex ratio island resemble the women of the high sex ratio island and reproduce with at most two men.

Discussion

There was a trend for this society to conform to Bateman's first principle of higher variance in fertility among men, although this was driven by the low sex ratio island; men and women on the high sex ratio island, where women are mate-limiting, had nearly identical variance in fertility. However, there was a trend for men on the high sex ratio island to vary more than women in their number of mates, Bateman's second principle, although this was not statistically significant. Both the lack of consistent sex

difference and the variation by sex ratio indicate that humans differ from Bateman's (1948) original prescription (see also Brown, et al., 2009), and indeed, Bateman's results imply a particular adult sex ratio (Kokko, et al., 2012).

Both Figures 5 and 6 highlight the role of monogamy in this society, although genetic analyses might yield a different pattern. Figure 5 underscores an additional point. The relationship between number of mates and fertility for men was similar for most men across both islands, indicating then even though women were scarce on the high sex ratio island, some men acquired multiple mates. High sex ratio societies are associated with early and stable marriages (e.g., Albrecht & Albrecht, 2001; Trent & South, 1989), and the returns for males to seeking additional mates are predicted to be low (Kokko & Jennions, 2008), so this similarity is surprising. The general pattern may have been similar, but there was one striking exception—one man was extraordinarily successful on the low sex ratio island, and it may be the case that a subgroup of men are indeed able to achieve particularly high returns to mating effort when there is an excess of women, as predicted by theoretical models (Kokko & Jennions). The otherwise similar pattern for the benefits to men's multiple mating across sex ratios may also explain why, if men's same-sex aggression is a form of mate competition (e.g., Archer, 2009; Daly & Wilson, 1990), there were no mean differences in men's same-sex aggression between the islands (Stone, 2015; see Schacht & Borgerhoff Mulder, 2014, for additional speculation about variation in this relationship).

For women, Figure 6 illustrates how closely linked variation in the adult sex ratio is to marriage and possibly paternal investment. Some women on the low sex ratio island married and had children with one man, whereas others—all unmarried women—had

each child by a different man (although a few married later in life). For these unmarried women, additional mates directly increased fertility. This suggests low adult sex ratios may be associated with sexual selection among some unmarried women. If so, it is unassociated with the use of same-sex physical aggression, although there do appear to be mating benefits to using indirect aggression on this island (see Chapter 3; see, also, Vaillancourt, 2013).

Also, this pattern for unmarried women on the low sex ratio island affirms the link between low sex ratios and nonmarital births in cross-national analyses (e.g., Barber, 2003) and bolsters behavioral data indicating men spend less time around their kids when more women are in camp (Marlowe, 1999). Together, these data indicate that men in low sex ratio societies likely provide less paternal care—indeed, on this island, some men appear to have provided minimal commitment—supporting recent theoretical predictions that men's mating effort should counter-intuitively increase with a surplus of women (Kokko & Jennions, 2008). These data also highlight why—in this society, it appears it may particularly benefit a subset of men.

Table 3

Adult Sex Ratio Effects on Bateman's First and Second Principles

	Low Sex Ratio			High Sex Ratio		
Measure	Men	Women	*F*	Men	Women	*F*
Mean Fertility	2.86	2.6		2.21	2.34	
Variance (Bateman's 1st Principle)	*12.34*	*4.87*	*2.53**	*6.24*	*7.23*	*0.86*
Mean Number of Mates	1.0	1.37		0.86	0.76	
Variance (Bateman's 2nd Principle)	*1.5*	*1.55*	*0.97*	*0.62*	*0.33*	*1.87†*

Note. † $p < .10$, * $p < .05$.

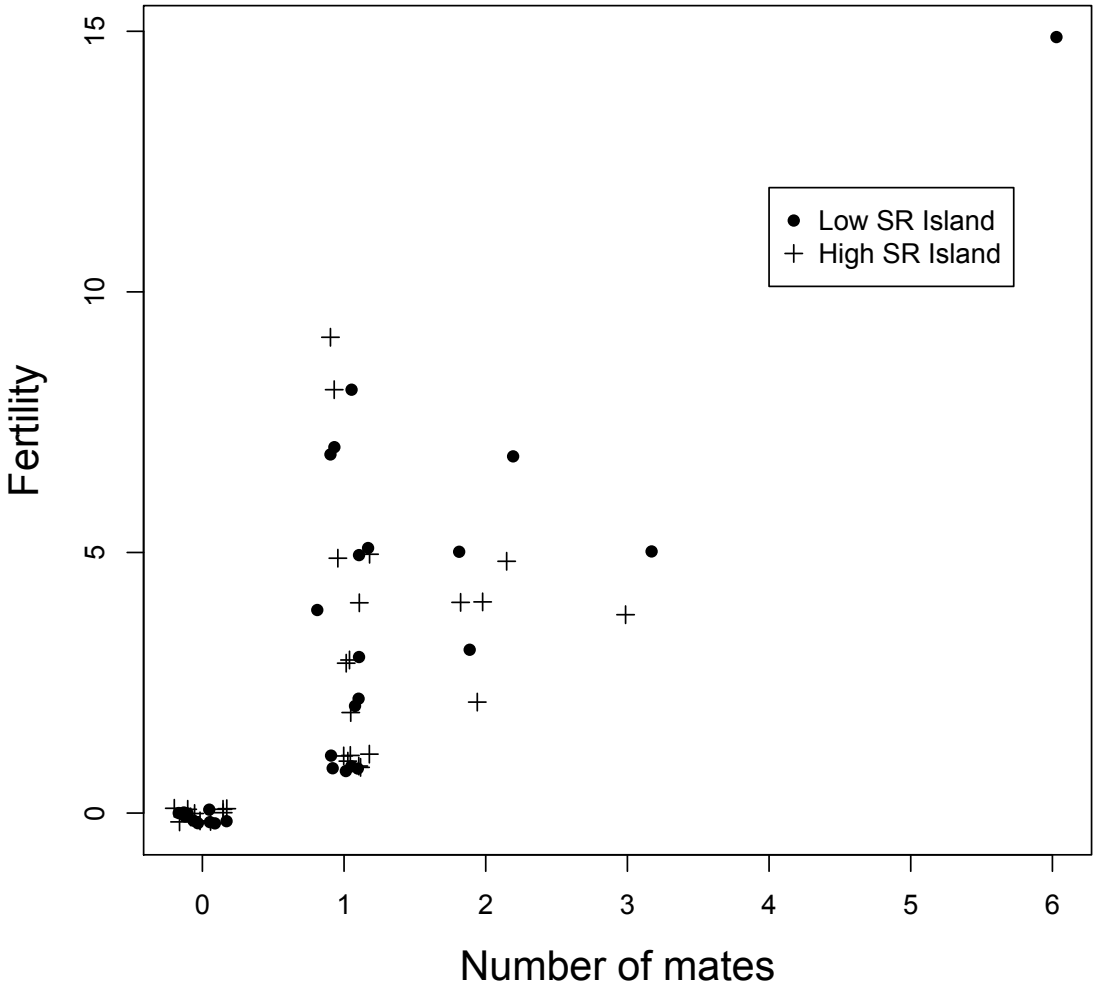

Figure 5. Bateman gradient by island for men.

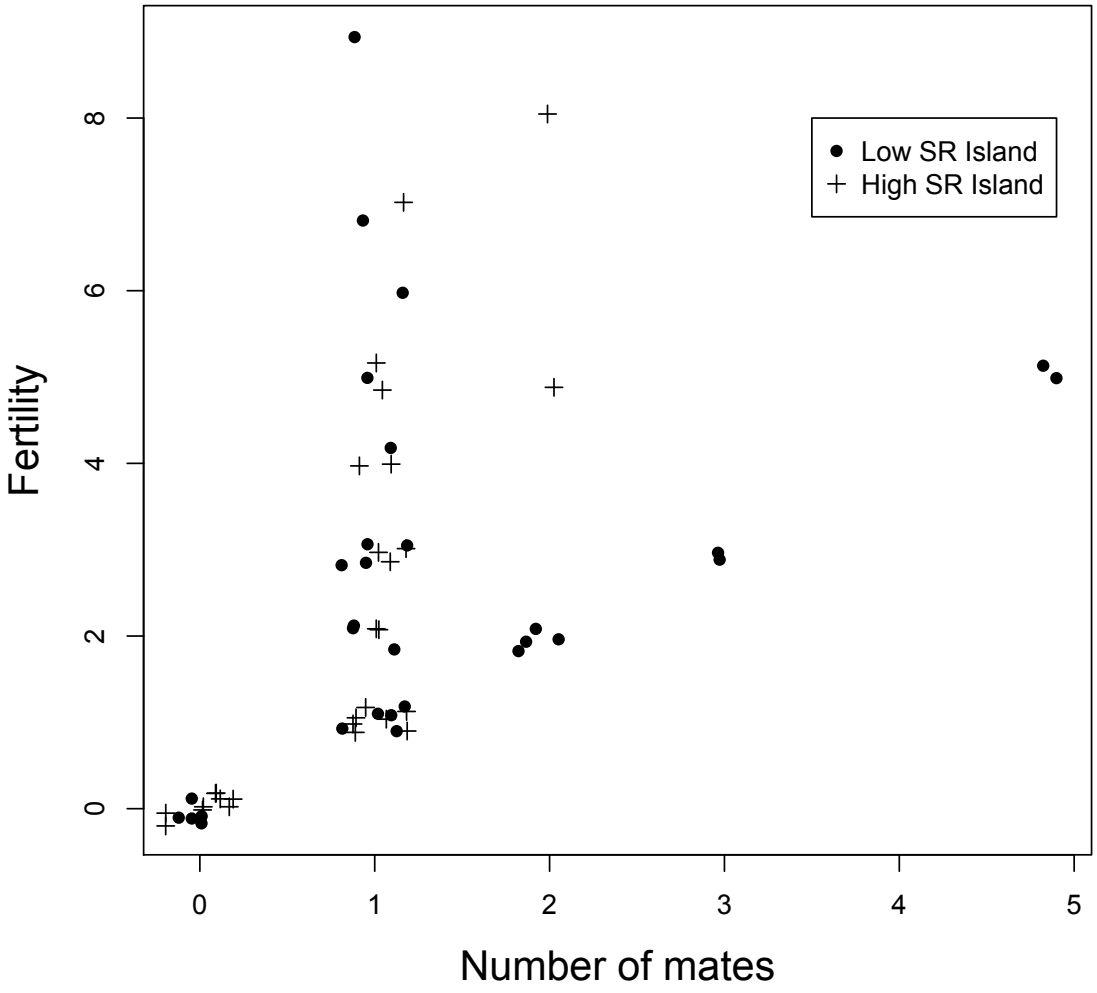

Figure 6. Bateman gradient by island for women.

CHAPTER V

CONCLUSION

This dissertation addresses the question whether and how women compete for mates in three main chapters. Chapter 2 was a review of the cross-cultural literature review on whether there is evidence that women increase the intensity of their mating effort when mates were scarce or plentiful. It found mixed results, and only one potential pattern within the variation, which suggested that perhaps traditional societies reduced variation in women's mating effort, to the extent men are better able to control women's behavior in those societies. It also highlighted the lack of consistency between potential measures of mating effort and the intensity and frequency of engaging in particular forms of mate competition. We clearly have a long way to go to understand patterns of women's mating effort.

The third chapter addressed the broader question of whether women use aggression to compete for mates by testing quantitative predictors of the intensity of women's same-sex aggression and the nature of the benefits to competition. The results suggest that women use indirect aggression in mating competition, but that it does not result in an increased likelihood of marrying or an increased number of mates. Other research indicates it effectively decreases the attractiveness of competitors (e.g., Vaillancourt, 2013), and this study indicated that it was associated with a younger age of

first marriage once interactions with the sex ratio were controlled. Thus, the mating benefits of using indirect aggression must interact with other variables, including, for example, physical attractiveness. The results of Chapter 3 also some evidence that women's use of physical aggression translates into higher fertility. They suggest that physical aggression resulted in offspring benefits on the low sex ratio island, and once the interaction between island sex ratio was controlled for, physical aggression positively predicted fertility. Thus, there is qualitative evidence that women use physical aggression in competition over men, but we have yet to establish a quantitative relationship. Much more research is needed to clarify predictors of women's mating effort. To this end, Chapter 3 indicates marital status is a factor in the outer islands of Yap.

Chapter 4 demonstrated how sex ratio imbalances affected Bateman's principles in one population. A high sex ratio reduced men's variance in fertility, indicating men were not monopolizing mating opportunities to the exclusion of other men any more than women were, on that island. A low sex ratio increased women's variance in the number of mates, which was made apparent in Figure 6. This suggested that men on the low sex ratio island are not sticking around after they father a child with some unmarried women, which supports aggregate data at the national-level that there are more out-of-wedlock births in low sex ratio societies. This pattern of results is consistent with the frequency-dependent returns hypothesis discussed and evaluated in Chapter 2. Chapter 4 provided additional evidence in support of the sensitivity of men's mating effort to respond to the available number of mating opportunities.

The preceding chapters add to our knowledge about sex ratio in several ways.

First, they provide data at the level of the individual, rather than in aggregate form, which constitutes most previous research on sex ratio imbalances. Individual-level data has provided the opportunity to explore interactions between the potential costs and benefits of aggression on both islands. To my knowledge, this is the first analysis to do so, and it supports predictions by Kokko and Jennions (2008). Chapter 3 also provides cross-cultural support for the use of indirect aggression in women's mate competition (Vaillancourt, 2013). Lastly, these chapters aim to explain women's competition, which has received comparatively less attention than men's and is evidently less well understood. Hopefully the questions, data, and analysis herein provide the contours to guide future work on women's aggressive competition.

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